4 Plant and Animal Activity Below the Solum

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ABSTRACT

If soil depth is defined by the depth of organism activity, then the generalized concept of useful soil depth is much too shallow. While climate and geologic features combine to limit the extent of biologic activity in some soils, this review indicates many instances where such activity continues to great depths. Arbitrarily selecting a 1.5-m lower limit to the solum, we review reports of plant root, root symbiont, and vertebrate and invertebrate activity below this depth. The evidence for plant activity is given by the mere presence of roots as well as observations of water and solute uptake. Water uptake evidence comes from (i) observations of plant roots in the capillary fringe, or at or beneath a water table, (ii) water depletion from unconsolidated regolith with no water table present, and (iii) presence of roots in saprolite and weathered or fractured rock. These observations are numerous and demonstrate root activity to a depth of 40 m under certain conditions. Solute uptake is less readily documented. The few occurrences reported generally range in depth from 2 to 3 m, with one for U at 20 m. Root symbionts (rhizobia and mycorrhiza-forming fungus) also are present at depth (3–34-m) but, like solutes, reports are few. The depth range for faunal activity is from several to 100 m. Clearly, the material below the solum, usually considered not affected by soil-forming processes, is often well inhabited by flora and fauna. The importance of these subsoil volumes is still unclear apart from water withdrawal, but obviously relate to the belowground environment and the adaptation of species to this environment. An excessive concentration of attention in the surface 20 to 40 cm of soil seems often unwarranted.

A vast literature treats activities of plant roots, microorganisms and larger fauna occupying the uppermost layers of the regolith. The numbers of roots and individual organisms in the upper 10 to 100 cm of soil usually are so great and comprise such a large proportion of the estimated totals that, for convenience, any residues below are ignored. Such is a common approach in many humid region investigations, not only of annual crop and pasture systems but also of forests. Indeed, many well-studied soils are underlain by materials that are so dense, so poorly aerated or so cold that roots and

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macroorganisms scarcely penetrate below, or even to, the lower boundary of the solum.

The present view, however, is concerned with less restrictive systems in which roots and some soil animals exploit portions of the regolith lying below an arbitrary depth of about 1.5 m, or a lesser depth where rock or saprolite occur closer to the soil surface. Thus the review title is misleading in those instances where contemporary pedological processes extend deeper than 1.5 m. This depth boundary, however, corresponds to that for the "deeper subsoil" as used by Kiesellbach et al. (1929), and conveniently excludes the overlying soil which also is part of the geologists' regolith.

Early studies of crop root systems, reviewed by Miller (1916), mostly were carried out in containers or limited to no more than solum depth. In North America, Goff (1897) early noted that apple roots reached depths >2.7 m. Major attention to deep roots, however, came about through the widespread sowing of alfalfa in the deep friable soils of eastern Nebraska in a climate where potential evapotranspiration (PET) exceeded mean annual precipitation.

Depending on soil and plant age, alfalfa roots were found to extend to 4 to >10 m deep, to deplete stored soil water (Alway, 1913; Alway et al., 1917; Alway et al., 1919), and to utilize groundwater (Burr, 1914). Alway (1913) and Alway et al. (1919), respectively, also observed relatively deep rooting by black locust and oak plantations adjacent to alfalfa fields they studied.[1]

Almost simultaneously, Weaver (1915) reported that several species of the native prairie on loessal soils of southeastern Washington had rooting depths of 2.5 to >3 m. Subsequent studies in the eastern Nebraska prairie and shrub associations revealed maximum rooting depths of 3 to 5 cm for many, but by no means all, native species (Weaver, 1919, 1920). He also examined many annual crop species (Weaver, 1920, 1926), finding that all of the grains (other than sorghum), as well as sunflower and sweet clover, extended roots below 2 m in some soils. Variation within, as well as among, species at the same location were evident, as were consistent differences among locations.

The following seven decades of investigation have vastly expanded both the number of species and the vegetation types known to root below the conventionally defined solum, as well as the maximum rooting depths attained. Alfalfa roots, for example, may reach depths of 39 m (Meinzer, 1927) rather than the 10 m mentioned above. A recent review (Stone & Kalisz, 1991) notes that roots of fruit trees extend 3 to 10 m deep where soil properties permit, that many forest trees and phreatophyte shrubs have similar capabilities and that, in a few instances, living roots have been found 30 to 60 m below the surface. Of particular interest, in view of many statements about forests of the humid Tropics, are reports of >3- to >12-m rooting depths there.

[1] Scientific names of plants and authorities are given in text when the species are not included in the tables.

The present review, however, treats exploitation of the deeper layers rather than maximum penetration. Observations of water uptake offer convincing evidence on this point. Three categories of uptake opportunity may be recognized: (i) from water tables or their capillary fringes, (ii) from unconsolidated regolith not influenced by a permanent water table although possibly by unsaturated flow on slopes, and (iii) from saprolite and weathered or fractured rock.

WATER UPTAKE

From Water Tables

Plants classed as phreatophytes tap groundwater at some depth, which may be from <1 m to many meters. Roots of salt cedar (tamarisk) examined by Gary (1963), for example, reached water at 3.7 m whereas Minckley and Brown (1982) stated that roots of velvet mesquite "cannot reach groundwater much below 14 m." Lowering water tables below that depth was held responsible for extensive death of mesquite woodlands in Arizona.

Many other species not classed as phreatophytes, or not regularly so, nevertheless exploit groundwater where it is available to functioning roots. Naturally subirrigated alfalfa on river terraces has maintained productivity in climates where upland plantings decline after exhausting the store of substrate water (Burr, 1914; Fox & Lipps, 1955).

Similarly, many tree species normally associated with well-drained habitats are found in contact with deep groundwater at least occasionally (Stone & Kalisz, 1991) and often unexpectedly (Kalisz et al., 1988). Some woody perennials of arid or seasonally dry climates access groundwater at remarkable depths (Table 4–1). With jarrah, a West Australian eucalypt, leaf water deficits in summer are similar to those of early spring, indicating adequate uptake by deep roots (Doley, 1967) which commonly reach watertables. The landscape significance of this sustained higher evapotranspiration (ET) has been revealed by the downslope emergence of saline groundwater from deep sources some years after conversion of jarrah forests to cropping systems with much lower annual ET. In the same region, Greenwood et al. (1985), estimated that plantations of *Eucalyptus maculata* Hook. and *E. cladocalyx* F.J. Muell. had an annual ET of 2300 and 2700 mm, respectively, when they had access to a water table -8 m, in contrast to 390 mm for heavily grazed pasture.

From Unconsolidated Regolith

In freely drained soils, reduction of the water content below field capacity (with allowance for rainfall) affords a cumulative measure of root activity. At the extreme, some large volume of substrate is brought near or below the 1.5-MPa (15-bar) wilting point. The alfalfa studies mentioned above provided an early demonstration of the depth and magnitude of such deple-

Table 4-1. Selected examples of plant roots in the capillary fringe, or at or beneath a water table at depth.

Species	Depth	Reference
	m	
Alfalfa		
Medicago sativa L.	4.3–5.5	Burr, 1914
M. sativa	3.5	Fox & Lipps, 1955
Grasses		
Spartina michauxiana Hitchc.	4.0	Weaver, 1915
Trees and Shrubs		
Juniperus monosperma (Engelm.) Sarg.	19.8	Cannon & Starrett, 1956, p. 391–409
Pinus elliottii Elgelm.	3.0	Schultz, 1972
P. sylvestris L.	5.0	Orlov, 1980
P. strobus L.	3.3	Stone, 1951, unpublished data
Casuarina equisetifolia JR & G. Forst.	4.0	Kaupenjohann & Zech, 1988
Phyllanthus emblica L.	5.8	Howard, 1925
Acacia raddiana Savi	35.0	Anonymous, 1974
Andira humilis Mart.	18.0	Rawitscher, 1948
Halimodendron halodendron (Pall.) Voss	>4.3	Chalidizo, 1965
Prosopis farcta (Soland.) Macbride	15.0	Schmueli, 1948
P. velutina Woot.	~14.0	Minckley & Brown, 1982
Quercus alba L.	3.4†	Kalisz et al., 1988
Q. douglasii Hock & Am.	24.0‡	Lewis & Burgy, 1964
Q. wislizenii A. DC.	24.0	Lewis & Burgy, 1964
Eucalyptus marginata Sm.	15.0	Kimber, 1974
E. marginata	19.0	Carbon et al., 1980
E. marginata	40.0	Dell et al., 1983
Tamarix pentatandra Pallas	3.7	Gary, 1963
Ulmus americana L.	6.1	Hayes & Stoeckler, 1935
U. pumila L.	4.8	Sprackling & Read, 1979

† ^{3}H uptake.
‡ ^{3}H uptake, 1.2 m soil over fractured rock.

tion. As Table 4–2 illustrates, a great number of species, notably perennials, utilize water at depths well below 1.5 m. The obvious consequences include greater ET losses from vegetations that root to these depths, greater plant productivity, increased substrate ventilation, and increased opportunities for precipitation or dehydration of materials deep in the substrate.

As Hoover et al. (1953) noted years ago, neither root concentation nor abundance may be a reliable guide to the rate or amount of water removed from a given soil depth. How water is extracted to low levels from soil volumes between roots spaced up to a few centimeters apart is uncertain. A role for mycorrhizae seems plausible where they occur, but evidence pro and con is reviewed by Reid (1991).

From Saprolite and Weathered or Fractured Rock

Observations in quarries, mines, caves and new roadcuts reveal that some species extend roots downward through interconnecting fissures and "soft spots" even to a depth of 60 m (Stone & Kalisz, 1991). Various investigators

Table 4-2. Maximum recorded depths of moisture depletion by plants from unconsolidated regolith with no water table present, selected examples.

Crop of species	Depth	Reference
	m	
Field Crops		
Alfalfa	10.0	Alway, 1913
Alfalfa (5–6 yr)	10.0	Kiesselbach et al., 1929
Alfalfa	6.4 (~wp)†	Alway et al., 1919
Wheat, *Triticum aestivum* L.	2.4	Kmoch et al., 1957
Corn, *Zea mays* L.	1.8 (~wp)	Fox & Lipps, 1960
Sunflower, *Helianthus annuus* L.	2.3	Georgen et al., 1991
Forbs		
Kochia scoparia L.	2.3	Georgen et al., 1991
Grasses		
Cynodon dactylon (L.) Pers.	3.2 (wp)	Russell, 1973
C. dactylon - Common, Coastal, Suwanee Bermuda		
Paspalum notatum Flugge	2.4	Burton et al., 1954
P. dilitatum Poir.		
Digitaria decumbens Stent.		
Cenchrus ciliaris L.	>6.0 (wp)	Dagg, 1969
Orchard species		
Malus sp.	10.7	Wiggans, 1935
Malus sp.	10.0	Yocum, 1935, p. 44–55
Prunus dulcis (Mill.) D.A. Webb	3.7	Hendrickson & Viehmeyer, 1955
Juglans regia L.	>3.6	Viehmeyer & Hendrickson, 1938
Coffea arabica L.	>3.0	Pereira, 1957
Camella sinensis (L.) Kuntze	>5.5	Laycock & Wood, 1963
Trees and shrubs		
Cupressus lusitanica Mill.	4.9	Hosegood & Howland, 1966
C. macrocarpa Hartw.	4.6	Pereira & Hosegood, 1962
Juniperus virginiana L.	>3.3 (~wp)	Sander, 1970
Picea abies (L.) Karst.	3.7	Horner & McCall, 1944
Pinus halapensis Mill.	4.5	Sanchori et al., 1967
P. lambertiana Dougl	>5.5	Ziemer, 1978
P. patula Schl. & Cham.	>6.0 (wp)	Russell, 1973
P. pinaster Ait.	7.0	Butcher & Havel, 1976
P. radiata D. Don.	4.0	Jackson et al., 1983
P. strobus L.	>7.6	Wiggans, 1935
P. taeda L.	>6.1	Patric et al., 1965
Acer saccharum Marsh.	2.7	Schneider et al., 1966
Gleditsia triacanthos L.	>3.3 (~wp)	Sander, 1970
Robinia pseudoacacia L.,	3.7	Horner & McCall, 1944
Eucalyptus saligna Sm.	>6.0 (wp)	Russell, 1973
Populus tremuloides Michx.	>3.0	Johnston, 1970
Quercus sp.	>4.6	Alway et al., 1919
Quercus spp. and *Carya* spp.	6.1	Patric et al., 1965
East African rain forest	>3.2	Pereira et al., 1962
Surinam high forest	>5.0	Poels, 1987

† wp = wilting point.

have described the ramification of roots in fractured rock. Hellmers et al. (1955), for example, figured the root distribution of some California chaparel species, noting that some species penetrated to depths of 8.5 m whereas

others, including some of the same genera, were consistently no deeper than 1 to 2 m below the soil surface.

Hellmers et al. (1955), Scholl (1976), Davis and Pase (1977) and others logically assumed that roots in rock were effective in water uptake but quantitative measures of such activity are limited. Table 4–3 exemplifies such evidence indicating significant water retention or uptake. Sustained activity of vegetation after exhaustion of available water in the overlying soil mantle (Fisher & Stone, 1968; M. Newton, 1992, personal communication) provides additional evidence.

As Table 4–3 indicates, the quantities of plant-available water are small on a volume basis but the total extractable from the rooting depth in rock may be greater than that in the overlying shallow soil. The additional water available to deep-rooted plants on shallow soils obviously influences the outcome of competition among species, and increases net productivity. Further, as watershed investigators have pointed out, water use by deep-rooted species can reduce water yields to a degree not predictable from characteristics of the surface mantle (Hellmers et al., 1955; Tew, 1966; Scholl, 1976; Davis & Pase, 1977).

Much of the foregoing also applies to saprolites insofar as they are readily penetrated by roots. Saprolite bulk densities are much lower than weathering rock, however, and water retention correspondingly higher. Thickness of the saprolite layer may vary greatly between adjacent slope positions as a result of geomorphic history (Stolt et al., 1992), and may accord poorly with the thickness of the overlying soil material. There appear to be few published accounts of root proliferation in deep saprolite although the presence of such roots doubtless has been recorded in many soil profile descriptions. For example, Stolt (personal communication, 1992) observed "few fine roots" throughout a gneissic saprolite that extended from a depth of 1.5 m to the rock surface at 3.9 m (Stolt et al., 1992).

Micromorphological and dye-transmission studies of a North Carolina mica schist saprolite demonstrated the presence of both root and faunal channels and their roles in water movement. At a depth of 2.0 m below the soil surface, about 1 m below the soil–saprolite interface, open channels (mostly between 0.1 and 0.5 mm) made up $<2\%$ of the saprolite volume. Yet they apparently accounted for 93% of water flow at saturation (K_{sat}). In addition, infilled channels, (2–5 mm in diam.), presumably originally formed by roots and earthworms, occupied about 11% of the volume and contributed to the unsaturated matrix flow (Vepraskas et al., 1991).

On occasion, roots extending deeply in fissured or fractured rock may make contact with a water table. Table 4–2 indicates that two species of oak absorbed tritiated groundwater from a depth of -24 m in fractured rock. The same authors (Lewis & Burgy, 1964) also reported that, in earlier studies, these species plus valley oak (*Quercus lobata* Nee) and black oak (*Quercus Kelloggii* Newb.) all absorbed from water tables at -7 to 13 m below the surface. The soil mantle at both sites was no more than 1.2 m thick. The authors concluded that all trees of the stand were operating to depress the water table during dry summers.

Table 4-3 Plant-available water in weathered rock and saprolite penetrated by roots, as estimated by field or laboratory methods.

Species or vegetation	Rock	Rooting depth below saprolite or rock surface	Water content	Reference
		m	m^3/m^3	
Quercus gambelii Nutt.	Mica schist, fractured	>1.9	0.10†	Tew, 1966
Q. turbinella Greene	Coarse-grain granite, weathered and fractured	~4.0	~0.03‡ ~0.20§	Scholl, 1976
Pinus ponderosa Laws. plus herbs	Metasedimentary, weathered and fractured	~1.0	0.057†	Newton et al., 1988, p. 4-5
Chaparral ± ponderosa pine	Granite, variously weathered	Variable	0.008–0.108¶	Jones & Graham, 1992
	Granite, weathered		0.096#	Krammes, as cited in Jones & Graham, 1992
Vitis sp.	Chalk	>0.7	0.16–0.23†	Cohen & Sharabani, 1964

† Extraction determined by neutron probe.
‡ Between −100 and −10 000 J/kg, estimated from author's figure.
§ Between −10 and −10 000 J/kg, estimated from author's figure.
¶ Between −100 and −15 000 J/kg, range related to bulk density.
# Between −33 and −15 000 J/kg.

ELEMENT UPTAKE

Mass flow of water to roots in deep soil, fractured rock or saprolite obsly transports any contained solutes, including those leached from the lying surface and counted as lost in ordinary lysimeter studies. Other esses facilitating element uptake are diffusion gradients around absorboots, and the solubilizing effects of root or symbiont exudates and decomtion products. A compilation of tracer uptake by various plant types merford et al., 1984) contains several instances of elements absorbed be1.0 m, including one from 3.6 m (Fox & Lipps, 1964).

The issue, then, is not whether deep roots absorb elements but in what ntities or with what consequences. In these respects tracer studies may lead, inasmuch as concentrations at the application site are often far greathan natural, and also override existing gradients of concentration with th. Thus a special interest attaches to Lipps and Fox's (1956) demonstrai that roots of intensively cropped alfalfa depleted native levels of extracle P to depths as great as ~3 m.

In most natural systems, distinguishing a separate role of deep roots in ake of untagged macronutrients is hopelessly confounded by internal and ernal recirculation. Such uptake may be inferred, however, where sure layers are strongly leached, or where substrate materials afford greater ractable concentrations of a nutrient than does the surface. Highly acidic ums over neutral to calcareous substrates are common in some regions. ain, element availability in saprolite might increase around weathering faces.

Excepting materials such as unweathered loess, volcanic ash, etc., the te of macronutrient uptake by deep roots probably is too small to replace ntinuous removal by harvested crops. In natural systems with effective recirlation, however, such uptake may counter the inevitable losses incurred erosion, leaching and fire.

In two known instances, plant concentration of marker elements can attributed only to root exploitation of a subsurface layer. Tiller (1957) served higher concentrations of Co, Ni, Mn and Ca in needles of firstneration radiata pine planted in sand overlying basaltic tuff at depths of 6 to 3.6 m than where the tuff was deeper. Likewise, root exploitation of -containing coal beds nearly 20 m below the surface resulted in elevated concentrations in needles of pinyon pine (*Pinus edulis* Engelm.) and juniper *Juniperus monosperma*) (Cannon & Starrett, 1956, p. 391–407).

OCCURRENCE OF SYMBIONTS

Legume nodules are often thought restricted to the upper soil layers, nd failure to find them there has been taken as presumptive evidence of heir absence. As early as 1915, however, Weaver (1915) reported nodules n roots of a prairie lupine at a depth of 3.3 m, and it is now evident that lepth per se does not limit nodule formation. Jenkins et al. (1988) recovered

rhizobia at depths of 12 to 13 m in a desert soil, as well as nodules on mesquite (*Prosopis glandulosa* Torr.) roots at depths of 3 to 7 m. These values, however, are eclipsed by finding relatively high populations of *Bradyrhizobium* together with small-root fragments of *Acacia albida* at a depth of 34 m (Dupuy & Dreyfus, 1992).

The mesquite species mentioned above bore vesicular arbiscular (VA) mycorrhizae at depths of 4.5 to 4.8 m above a water table at 5.0 to 5.6 m (Virginia et al., 1986). The maximum depth for ectomycorrhizae known thus far is 15 m, on roots of *Eucalyptus gomphorcephala* DC. in a limestone cave (Lamont & Lange, 1976). A summary of reported occurrences on other species indicates depths no greater than 2 to 3 m (Stone & Kalisz, 1991), although that may be only the limit of purposeful examination. It seems probable that, when sought, N-fixing symbionts, mycorrhizae, rhizosphere organisms and fungal hyphae distant from roots will be found associated with many plant species roots deeply in well-aerated substrates.

ANIMAL ACTIVITY

Investigations of animal activity below the solum has produced a series of reviews detailing the complexity and myriad activities of soil fauna. Those in English range from Taylor (1935), Jacot (1940) and Thorp (1941) to Hole (1981) and Meadows and Meadows (1992), with many major accounts in between. Understandably, the overwhelming attention has been to the upper soil layers although deeper penetration, notably by termites, is treated in some (Lee & Wood, 1971).

The following brief review is illustrative rather than comprehensive and draws on the foregoing as well as original references. There are two initial premises: (i) in the absence of special studies only the larger animals, the macro- and megafauna of some authors, are likely to be observed; and (ii) information is largely limited to observation of burrows and krotovinas, with little on actual populations of organisms or their geomorphic influence.

Vertebrates

Some fossorial rodents mix the upper layers of soil so thoroughly, and are so numerous as to alter its morphology and development over appreciable areas (Borst, 1968; Kalisz & Stone, 1984). Burrows refilled with soil from another horizon or otherwise differentiated appear as krotovinas and mark the lower limits of activity. In well-drained substrates, some rodents, as well as other vertebrates, regularly burrow deeper than the 1.5-m upper limit of this review (Table 4–4). They carry down food and nest materials, may leave feces and skeletons, and augment soil ventilation in the vicinity of the burrow. A variety of other animals may use these burrows, either after abandonment, as with prairie dogs, or in association with the occupant, as with the gopher tortoise. Over 300 "other species" have been found using tor-

Table 4-4. Selected examples of faunal activity below 1.5-m depth.

Group or taxon	Maximum depth	Comment	Reference
	m		
Vertebrate			
Prairie dog (*Cynomys ludovicianus*)	>4	(Also rattlesnakes	Merriam, 1901
	~1–4.3	and owls)	Sheets et al., 1971
Gopher (*Thomomys* sp.)	0.5–>1.5		Moore & Reid, 1951
Gopher tortoise (*Gopherus polyphemus*)	2.8	(Also snakes,	Hansen, 1963
	6	beetles and frogs)	Burke & Cox, 1988
Invertebrates			
Earthworms			
Lumbricus terrestris	1.8–2.4		Darwin, 1991
Lumbricus (?)	>4		Weaver, 1915
(Undetermined)	3.6	(To water table)	Weaver, 1920
Lumbricus terrestris *Allobophora nocturna*	1.5–2.4		Edwards & Lofty, 1977
Scherotheca sp.	5.2		Lee, 1985
Octochaetus multiparus	3–5		Lee, 1985
Drawida grandis	~3		Gates, 1972
Tonoscolex birmanicus	~2.1		Gates, 1972
Crayfish			
(Undetermined)	4.6	(La.)	Thorp, 1941
(Undetermined)	~2	Typic Ochraqualf (Texas)	USDA, 1990
(Undetermined)	1.5	Typic Haplaquoll (Illinois)	Soil Survey Staff, 1975
Procambarus rogersi rogersi	>1.5	Typic Albaqualt (Florida)	Stone, 1993
Beetles			
(Dung beetles, Rhodesia)	1–2	(Buries dung)	Wood & Lee, 1973
Peltetrupes youngi	3.6	(Moves P to surface)	Kalisz & Stone, 1984
Typhaeus typhoeus	1.5		Brussard, 1983
T. liotius	1.6		Brussard, 1983
Ants			
Formica fusca	~1.5	(Moves clay and $CaCO_3$ to surface)	Levan & Stone, 1983
F. exsectoides	>2		Muckerman, 1902
Pogonomyrex badius	2.2		Gentry & Stiritz, 1972
Atta texana	~0.5 to 3.6–4.6		Creighton, 1950, p. 585
A. sexdens	>4		Eidmann, as cited in Weber, 1972
	~4	(Into saprolite)	Branner, 1900, 1910

(continued on next page)

Table 4-4. Continued.

Group or taxon	Maximum depth	Comment	Reference
	m		
Veromessor pergandei	~3		Sudd, 1967
Monomorium sp.	10		Cited by Cloud et al., 1980
Myrmecocystus melliger	4.9		Creighton & Crandall,1954
Termites			
(Undetermined)	8.6		Cited in Lee & Wood, 1971
Anacanthotermes ahngerianus	10-15		Dimo, 1910; as cited in Lepage et al., 1974
Psammotermes hybostoma	47		Lepage et al., 1974
Bellicositermes bellicosus	40-55		Lepage et al., 1972

toise burrows at least occasionally (Burke & Cox, 1988) and many of these thus qualify as residents of the deeper subsoil.

Dens of larger animals such as badgers, foxes, wombats, etc. (see also Endroma, 1988) sometimes extend below 1.5 m but their numbers are few and the affected area small. Moreover, it appears that some den sites are reoccupied over long periods, even thousands of years (Dunesman, 1967), further limiting the cumulative area of disturbance. Prior to settlement, prairie dogs were exceedingly numerous in parts of American grasslands, often forming large "towns" with characteristic vegetation (Koford, 1958). Some entrance mounds—and hence burrows—are centuries old (Carlson & White, 1987, p. 78). Thorp (1948) noted that, at one point, the surface soil texture had been changed from silt loam to loam by sand (and gravel) brought from depths of 2 to 3 m by prairie dogs and badgers.

Crayfish

Terrestrial crayfish, when active, must maintain contact with groundwater or pools retained within their burrows. This obviously affects depth of burrowing and also limits their distribution in the landscape. In the USA, species are numerous and reports of their works are commonly unaccompanied by species identifications. Apart from the life history accounts of some systematists, knowledge of crayfish presence, current or past, in the deeper subsoil is chiefly contained in soil profile descriptions (Table 4-4). The cylindrical krotovinas are characteristic, frequently they are thinly lined with clay or dark organic material.

Crayfish densities can be high. Taylor (1935) cited an unpublished U.S. Biological Survey manuscript that reported 3.6 holes per square meter in the surface of a Mississippi field. Although Thorp (1941) observed burrows 4.6 m deep in Louisiana, most reports are of much shallower depths. For

example, the description of a Ciena soil, a Typic Ochraqualf in southwest Texas, indicated that visible crayfish krotovinas comprised 35% of the soil area at 0.6- to 0.9-m depth and 15% at 1.2 to 1.4 m, with only "some evidence" at ~2 m (USDA-SCS, 1990). The investigators considered that crayfish burrowing decreased soil permeability by disrupting structural units. It seems likely that either filled or open burrows facilitate deep penetration of woody roots that are tolerant of anoxia but this has not been demonstrated.

Earthworms

Although many earthworm species are confined to near-surface layers, some penetrate well below the solum when circumstances are favorable (Table 4–4). Weaver (1915) characterized certain prairie sites in eastern Washington as "literally honeycombed" with 7- to 8-mm diam. channels to a depth of >4 m by a "species of Lumbricus." Again, in an eastern Nebraska prairie he found "countless earthworm burrows" extending as far as a water table at 3.6 m (Weaver, 1920). Both soils were friable.

Darwin (1881) observed that *L. terrestris* moved small pebbles, seeds and even marker beads from the surface to the bottom of its burrow. Movement of surface-applied materials, such as ^{137}Cs and dichloradiphenyl trichloroethane (DDT) to lesser depths have since been reported (Lee, 1985) and may well extend to the full burrow depth. A profile description of an Entic Haplustoll in Texas noted vertically oriented calcium carbonate nodules to depths of ~1.7 m that seemed to be filled channels of earthworms or termites (Soil Survey Staff, 1975, p. 670). Open channels, of course, facilitate subsoil ventilation and root pentration, and vertical roots are often seen to follow filled burrows.

Beetles

Reports of deep-boring beetles are uncommon (Table 4–4). In Florida, however, a scarab, *Peltotrupes youngi*, constructs 5- by 15-cm larval chambers >1 to 3.6 m deep in well-drained sands, and provisions them with organic detritus. Charcoal fragments from the surface can be so emplaced at depth. Vertical tunnels through sands with bulk densities of 1.7 to 1.9 kg m^{-3} appear to influence tree root penetration (Kalisz & Stone, 1984).

One of a related group of European dung beetles, *Typhaeus typhoeus*, burrows to lesser depths, ~0.3 to 1.5 m. It backfills its burrows which remain as meniscately patterned krotovinas, indicating its presence even in the Alleröd period, <11 000 yr ago. These <14-mm diam. krotovinas are seen to disturb initial bedding of sands and, elsewhere, to perforate subsoil lamellae (Brussaard & Runia, 1984), as do the galleries of *Peltotrupes*.

Ants

This group is enormously diverse in the habitats occupied, and the resources exploited. Relative to the total number of species, relatively few

penetrate very far below the solum (Table 4–4), although those that do may have profound effects. A fungus grower, *Atta sexdens*, the sauba ant of eastern Brazil, moves great quantities of subsurface materials into 1- to 4-m high nest mounds (Branner, 1900). It penetrates into saprolite where this occurs within reach, obviously increasing its macroporosity and altering weathering of the transported substrate. The related Texas leaf-cutting ant seeks a suitable sandy layer for its nest even though this may be ~4 m below the surface. In hot desert soils, *Veromesser pergandei* burrows extend ~3 m. Cloud et al. (1980) cite references to yet deeper penetration by some species to establish contact with a water table.

Termites

Lee and Wood (1971) have summarized the extensive literature on termite–soil interactions, including activity below the solum and instances of root development deep into filled galleries. Yakushev (1968) noted similarities between the wall structures of termite nests and perforated laterite in Mali, and proposed that the latter had formed by mineral replacement of the former.

Some African and central Asian desert and dryland species extend galleries to remarkable depths in order to reach free water (Table 4–4). Lee and Wood (1971) mention 70 m whereas Cloud et al. (1980) cite an unpublished report (by M. Lucher) of penetration to ~100 m.

Such extreme depths appear limited to a few species and habitats. Many species, however, mine dead or even live roots in the upper soil layers, and some, presumably, continue downward. In turn, roots exploit low-resistance passages in dense materials, as well as responding to local gradients in nutrients and soil gases. Explanation of the extraordinarily deep roots of some savanna and desert species (Table 4–1 and 4–2) may have to consider prior excavation by termites or, perhaps, alternate occupancy of extending passages by root and insect.

SYNOPSIS

Our arbitrary division of the regolith at 1.5 m has no meaning apart from convenience and emphasis. The significant boundaries for occupancy by plant roots and animals are between strata that are penetrable or impenetrable where these occur at depths less than the maximum capabilites of the species (suggested by Table 4–1 through 4–4).

Roots penetrating below the conventionally defined solum or any assumed "working depth" provide access to a greater volume of stored soil water or sometimes to phreatic sources. Such extension also increases the total mineral particle surface available for nutrient extraction, and often means a longer season of activity for both roots and their symbionts. Water uptake at depth facilitates recovery of nutrients leached from surface layers, as well as absorption from less highly weathered substrates or different miner-

al suites than those found at the surface. The possible consequences for the occupying vegetation are numerous: competitive advantage—or even sheer existence—for species able to exploit substrate resources, greater organic productivity, and expansion of the theater in which nutrient uptake and recirculation occur. Deep root penetration by trees usually increases resistance to windthrow, as well as the stability of steep or slip-prone slopes.

Many vertebrates as well as invertebrate species either burrow below the solum or use existing burrows and root channels. Such burrows have a variety of functions but all protect their occupants against extremes of surface temperature and humidity, and may allow use of downward temperature gradients. Some dryland termite and ant species extend tunnels to a water table, as do nondormant crayfish, whereas many other primary burrowers avoid periodically saturated soils.

Root penetration is constrained by soil strength, by adverse chemistry and, for most species, by adequacy of ventilation. In turn, however, withdrawal of water enlarges the cross-section available for gaseous diffusion, and any shrinkage with drying opens continuous pathways for both ventilation and further root penetration or thickening. Other evident consequences of deep soil drying are precipitation of solutes such as Ca and SO_4, and oxidation of reduced substances.

Like root channels, animal burrows are pathways for rapid gas exchange, except as gallery walls may be sealed. Roots, however, can only penetrate existing pores, and enlarge only by displacing surrounding soil. In contrast, burrowing animals actively mine tunnels, sometimes in material impenetrable to roots. Transport of the mined spoil to or near the surface obviously lowers gross bulk density of the substrate and may increase available nutrient content of the solum. With almost all species there is some addition of organic materials at depth, which must affect mineral weathering directly as well as through eventual proliferation of roots.

Inaccurate assumptions about shallow rooting depths or depths of biotic activity may have little consequence where the assumed depths are close to the actual limits of penetrability, as would be true, for example, for many soils over firm glacial tills or clayey sediments. In other large regions, however, ecological studies based on assumed depths may vastly underestimate resources available to past and present ecosystems, and ignore the action of plants and animals upon underlying layers of the regolith.

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